Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE DEVELOPMENT OF THE EMBRYO OF ENCEPHALARTOS

W. T. SAXTON

(WITH PLATE II AND ONE FIGURE)

Toward the close of 1906 Dr. H. H. W. PEARSON offered to turn over to me some material collected[1] with a view to following the development of the proembryo and embryo of Encephalartos. We hoped to publish a joint paper, of which the present account, completed two years ago, was to have been my contribution. As Dr. PEARSON now finds that the publication of his share will have to be delayed still further, he has suggested that I should publish the account separately. I am glad to take this opportunity of thanking him for his help, and especially for the drawings to which his initials are appended. I also wish to thank Professor SEWARD for assisting me with the microphotograph from which *fig. 18* is reproduced.

All sections were cut with a Cambridge rocking microtome, except that from which *figs. 16* and *17* were drawn, which was cut by hand. All figures were drawn with the aid of a Zeiss camera lucida, microscope, and lenses, except *fig. 18*, which is from a microphotograph. *Figs. 1, 2, 6–8, 12–15* were drawn by Dr. PEARSON, the others by myself.

The material at my disposal afforded a fairly complete series of the development of the embryo, but the stages to illustrate the proembryo and early post-fertilization stages are almost entirely wanting and will not be referred to. The first account of embryo development in cycads seems to have been that by WARMING[2] for Ceratozamia, but only a very few stages are described and figured. Proembryo development has been described in Cycas by TREUB[3] and

---

[1] With the aid of a grant from the British Association for the Advancement of Science.

[2] WARMING, E., Undersogelser of Betragtninger over Cycadeerne. 1877.

[3] TREUB, M., Recherches sur les Cycadées. 3. Embryogénie du *Cycas circinalis*. Ann. Jard. Bot. Buit. 4:1–11. *pls. 1–3*. 1884.

IKENO,[4] and in Zamia by COULTER and CHAMBERLAIN,[5] but later stages have not been closely followed for any cycad, and the results now presented fill in some of the gaps still remaining in our knowledge of this interesting group.

Description

The intraseminal development of the embryo for descriptive purposes may be divided into four stages, each of which passes gradually into the next: (1) the differentiation of a small mass of meristematic tissue at the base of the proembryo; (2) the rapid division and elongation of a group of cells at the proximal end of this meristematic tissue, forming the suspensor; (3) the differentiation of the cotyledons and stem apex; (4) the development of plumular leaves and the fusion of the distal halves of the cotyledons.

The youngest stages figured are from the embryos of *Encephalartos villosus* (*figs. 1, 2*). *Fig. 1* represents a stage in the development of the suspensor, the embryo being shaded. *Fig. 2* is drawn from a slightly older embryo, showing the latter in detail and a small part of the suspensor. The small group of actively dividing cells, about 40–50 in number (12–16 in sections), which is forming the suspensor, can be recognized readily by the fact that the cells are arranged in regular longitudinal rows.

The remaining figures (*3–18*) are from embryo of *E. Friderici-Guilielmi.*[6] *Fig. 3* represents the only case met with in which the suspensor was branched, the branches bearing two equally developed embryos. The figure shows the two branches of the suspensor only up to the point of junction; the suspensor was injured in sectioning just above this point, and it is impossible to say whether the branching is dichotomous or monopodial.

Fig. 4 is an outline of a longitudinal section of an embryo at the close of the second stage of its development. The part inclosed by a

[4] IKENO, S., Untersuchungen über die Entwickelung der Geschlechtsorgane und der Vorgang der Befruchtung bei *Cycas revoluta.* Jahrb. Wiss. Bot. 32:557–602. *pls. 8–10.* 1898.

[5] COULTER, J. M., AND CHAMBERLAIN, C. J., The embryogeny of Zamia. BOT. GAZETTE 35:184–194. *pls. 6–8.* 1903.

[6] This appears in *Index Kewensis* as a synonym of *E. cycadifolius,* but Dr. PEARSON informs me that he finds the two species to be quite distinct.

dotted line is drawn in detail in *fig. 5*. The group of suspensor-forming cells has now become the root meristem, and is not sharply differentiated from the distal part of the suspensor. At this stage cell division has recommenced in the distal half of the embryo, though as yet no further differentiation has taken place.

The first appearance of the cotyledons is shown in *fig. 6*. They clearly arise, as described for Ginkgo by LYON,[7] by the more rapid growth of two groups of cells of the distal meristem. The cotyledons of Pinus also are initiated by the more rapid growth of groups of cells of the apical meristem,[8] and it is probable that this is normally the case in all gymnosperms. The dermatogen is distinct at this stage, and the root meristem is more clearly shown than in *fig. 5*. The latter point is shown better in *fig. 7*, where the central part of *fig. 6* is drawn in detail.

Figs. 8, 9, and *10* show later stages, in which the principal changes are the elongation of the cotyledons and the development of the canals. The first indications of the formation of canals can be seen in the stage outlined in *fig. 9*, and their position is indicated in *fig. 10*. The canal marked x in *fig. 10* is drawn in detail in *fig. 11*. The dense contents contain tannin, and probably mucilage also, though it is not easy to demonstrate its presence. The canals are formed lysigenously, that is, by the breaking-down of rows of cells. The boundary of the root meristem is indicated by a dotted line in *figs. 9* and *10*. In the stage represented by *fig. 10* the tissue lying between the apical meristem and the root meristem is beginning to lose its meristematic character; the cells of this region are somewhat flattened longitudinally. *Figs. 12–15* show the outline of transverse sections of an embryo of approximately the same age as that drawn in longitudinal section in *fig. 10*. *Fig. 12* shows the base of the cotyledons and their attachment to the stem; *fig. 13* is taken just below the stem apex; *fig. 14* is somewhat higher up; and *fig. 15* is near the apex of the cotyledons. The principal point shown by this series is that at this stage the cotyledons are fused only in the proximal half of their length.

[7] LYON, H. L., The embryogeny of Ginkgo. Minn. Bot. Studies 3:275–290. *pls. 29–43*. 1904.

[8] The writer hopes to publish later an account of the development of the embryo in Pinus.

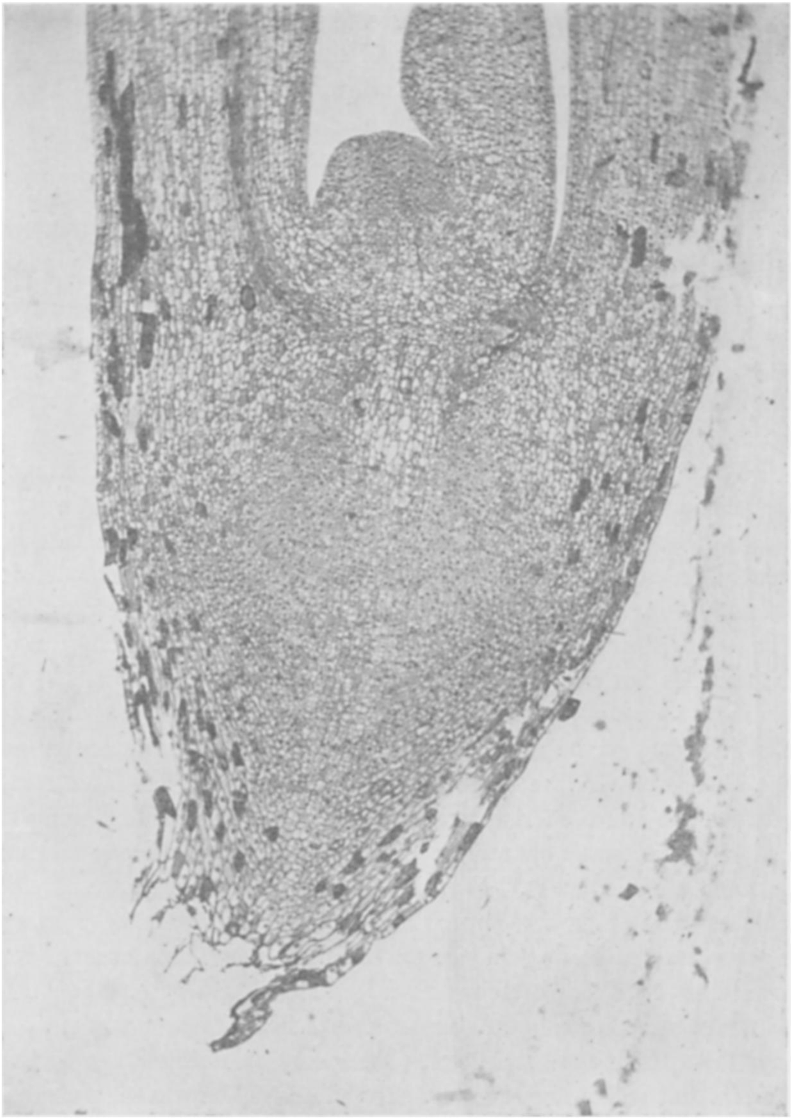


FIG. 18.—*E. Friderici-Guilielmi:* microphotograph of part of a longitudinal section of a nearly mature embryo. ×50.

In the last stage of intraseminal development the primordia of one or two plumular leaves reach a moderate size. The cotyledons in the mature embryo are fused throughout their whole length, by both margins at the base, and by either one or both margins near the apex. *Fig. 16* represents a transverse section in which they were fused by one margin only; the part of the section marked *x* is drawn in detail in *fig. 17*. This shows the very intimate union of the epidermal cells and their collenchymatous thickenings.

Fig. 18 represents the root and stem apices, the bases of the cotyledons, and the first plumular leaf. The root meristem has now increased considerably in size, but has not otherwise changed its character in any way, so that what is physiologically the root cap is only the distal end of the suspensor as morphologically equivalent to part of the root cap of any ordinary angiospermous embryo. The embryonal tubes in certain conifers are evidently equivalent to the whole suspensor of Encephalartos.

From the preceding account it is clear that there is a very close resemblance between the embryogeny of Encephalartos and that of Ginkgo as described by Lyon (*l. c.*).

Summary

1. The suspensor is developed by the division and elongation of a group of cells at the proximal end of the embryo.
2. This group of cells forms later the root meristem.
3. Branching of the suspensor has been observed once, resulting in the formation of two approximately equal embryos.
4. The cotyledons are initiated by the more rapid growth of two groups of cells of the apical meristem.
5. The canals appear before the differentiation of plumular leaves, and probably contain both tannin and mucilage, being formed lysigenously.
6. A very intimate connection is established between the epidermal cells of fusing cotyledons.
7. The suspensor is morphologically a root cap.
8. The embryogeny of Encephalartos is very similar to that of Gingko.

South African College
Cape Town

EXPLANATION OF PLATE II

Encephalartos villosus

FIG. 1.—Suspensor carrying down young embryo (shaded) into the endosperm; *aw*, archegonium wall. ×77.

FIG. 2.—Young embryo slightly older. ×310.

Encephalartos Friderici-Guilielmi

FIG. 3.—Branching of the suspensor forming two approximately equal embryos. ×77.

FIG. 4.—Outline of embryo and part of suspensor, just before differentiation of cotyledons. ×40.

FIG. 5.—Detailed drawing of part of *fig. 4* indicated by dotted line. ×300.

FIG. 6.—Cell outline of embryo just after differentiation of cotyledons. ×117.

FIG. 7.—Detailed drawing of part of *fig. 6;* junction of root and stem meristems. ×300.

FIG. 8.—Outline of slightly older embryo. ×24.

FIG. 9.—Older embryo than *fig. 8;* root meristem outlined with dotted line. ×40.

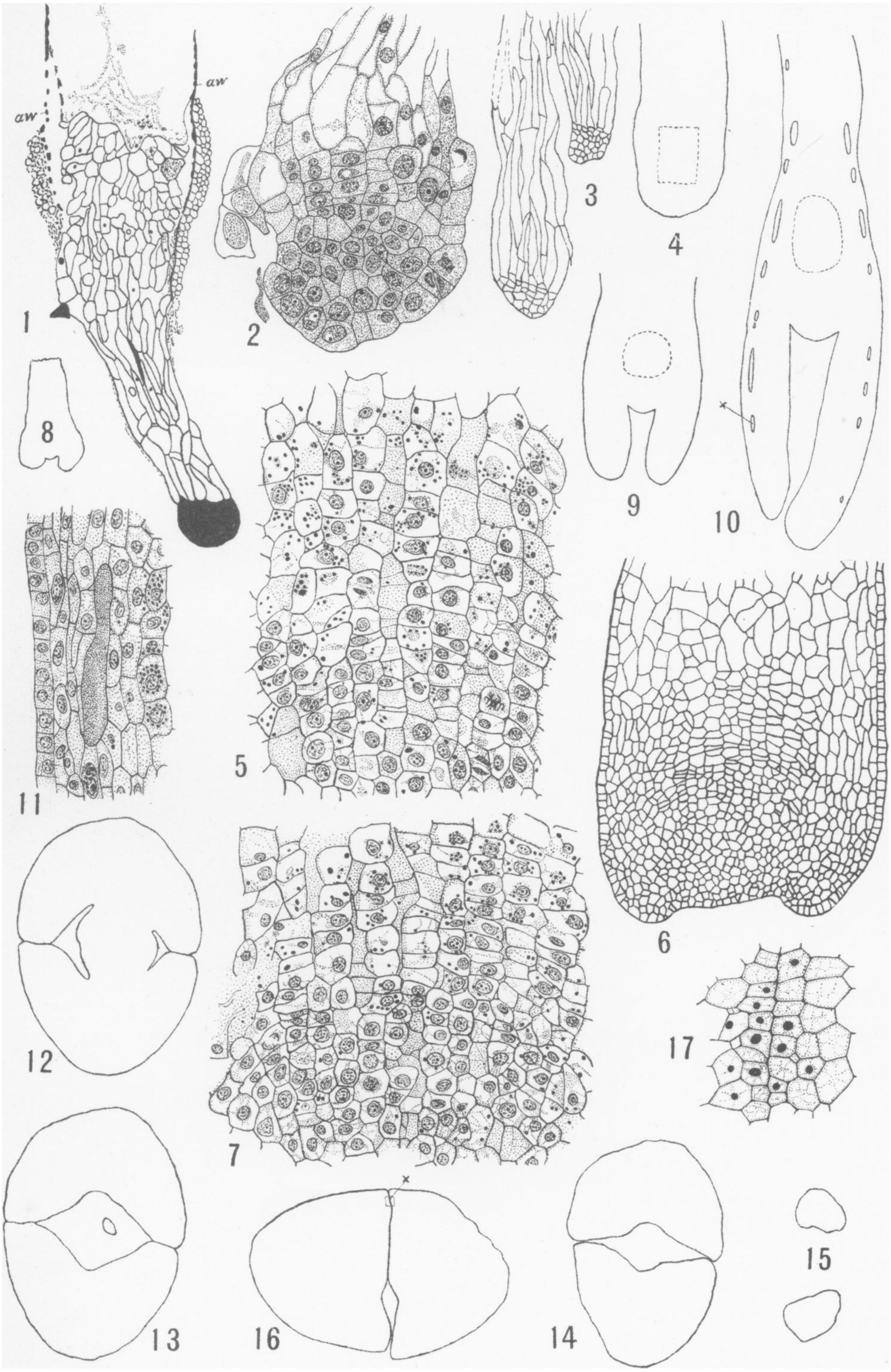
FIG. 10.—Embryo older than *fig. 9;* canals outlined, that marked x shown in next figure. ×40.

FIG. 11.—Canal from *fig. 10* drawn in detail. ×310.

FIGS. 12–15.—For explanation see text.

FIG. 16.—Cross-section of cotyledons of a mature embryo. ×24.

FIG. 17.—Part of *fig. 12* marked x drawn in detail. ×310.



SAXTON on ENCEPHALARTOS